

ON  
*PROTEOCEPHALUS MARENZELLERI*,  
*P. NAIÆ* AND *P. VIPERIS*

BY  
W. N. F. WOODLAND

*Wellcome Bureau of Scientific Research, Endsleigh Gardens,  
London, N.W. 1*

*(Received for publication May 25, 1925)*

***PROTEOCEPHALUS MARENZELLERI* (Barrois, 1898)**

This species, one of the largest known Proteocephalids, was first proposed (as *Ichthyotaenia marenzelleri*) by Barrois (1898) who supplied a very brief account of its structure from material collected by Calmette in 1897 from *Ancistrodon piscivorous* Holbr., the 'Water Viper,' a snake found in the southern United States. Ten years later, Schwarz (1908) published a more complete description, with three figures, solely based, however, upon the identical material studied by Barrois. Five years later still, Beddard (1913b) supplied some further details of structure from the examination of a number of immature specimens (the longest measuring about 250 mm.) found in a water viper which had died in the London Zoological Gardens. Since Beddard's specimens were immature and La Rue (1914) expressly recommends a further study of new material, the following description of the anatomy of one large fully-mature example, which I have found recently in the Wellcome Bureau collection of Helminths and which was collected from a water viper which had also died in the London Zoological Gardens, is worth publishing.

My single specimen measured between 300 mm. and 400 mm. in length and was well preserved in spirit. It shows well a striking feature of this species, viz., the very small proportion of the strobila which consists of mature and ripe proglottides. As Beddard remarks concerning his specimens, 'in proglottides situated 8 inches or so

from the scolex [the largest worm being 10 inches in length in spirit] there were merely traces of the reproductive organs,' and in my own single specimen, though it must have measured about 350 mm. (i.e., over 14 inches, in spirit) in total length, yet I did not obtain from the strobila more than about a dozen ripe proglottides and as many which could be described as mature, the rest of the strobila consisting of immature proglottides.

The scolex (fig. 1) was present and measured about 1.9 mm. in breadth. The four large suckers are borne on protrusible lobes on the anterior end of the scolex and face upwards and outwards, the apex of the scolex being quite insignificant, i.e., no 'rostellum' is present. I did not sectionize the scolex to ascertain if a minute apical organ were present. The suckers measure about 0.913 mm. in breadth. Spinelets are entirely absent. The unsegmented neck is about 7 mm. long, with an average breadth of about 1.4 mm.

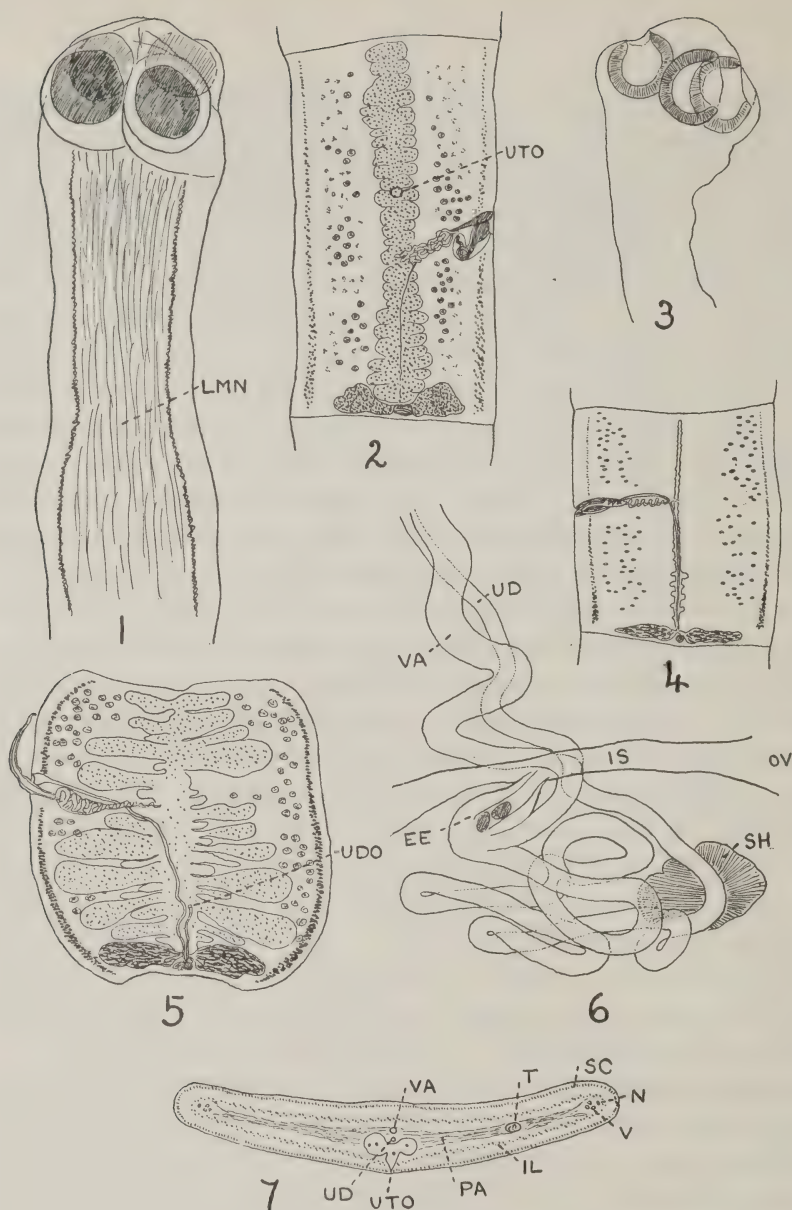
The strobila is, in transverse section, extremely flat and has a maximum breadth of a little over 3 mm. (3.068 mm.). The immature proglottides which, as already stated, compose by far the greater part of the strobila, vary in size and shape from  $\frac{1.9 \text{ mm. broad}}{0.767 \text{ mm. long}}$  in front to  $\frac{3.068 \text{ mm. broad}}{1.180 \text{ mm. long}}$  behind, and thus are all broader than long. Mature proglottides are more square in shape ( $\frac{2.95 \text{ mm. broad}}{1.71 \text{ mm. long}}$  and  $\frac{2.8 \text{ mm. broad}}{2.0 \text{ mm. long}}$ ), while ripe proglottides are, more anteriorly, distinctly broader than long ( $\frac{3.068 \text{ mm. broad}}{1.8 \text{ mm. long}}$ ) and, more posteriorly, longer than broad ( $\frac{2.124 \text{ mm. broad}}{4.0 \text{ mm. long}}$ ). The genital apertures are, as usual, irregularly alternate and open midway in the lengths of the proglottides, and the cirrus and vaginal apertures irregularly alternate as to which is anterior. The cirrus sac in mature and ripe segments is extremely broad antero-posteriorly, measuring 0.448 to 0.680 mm. in length and 0.149 to 0.298 mm. in maximum breadth. In some proglottides the sac stretches over a quarter of the breadth of the proglottis but usually a somewhat less distance. The contained cirrus is, next the opening, bulbous in form, and continuous with a straight portion which is connected with several coils of the ductus at the base of the sac. The cirrus was not everted in any of my preparations. The vas deferens

outside the sac is not very voluminous and stretches to the middle line of the proglottis. The vagina is dilated only next its opening. Occasionally a small genital atrium or depression seems to be present, but usually the two apertures appear to lie next the surface at the same horizontal level. The young ovary is rather flattened antero-posteriorly but becomes less so in ripe proglottides, and is of the lateral extent shown in fig. 2. The isthmus joining the two lobes of the ovary is thin and canalicular when seen in toto-preparations and the entire ovary is seen to be very flat in transverse sections. Both the uterine canal and the vagina lie dorsal to the ovarian isthmus (the vagina being ventral to the canal in front of the ovary) and a shell-gland is present. The testes are numerous and lie in two lateral fields and measure on an average about 44 by 22 microns. The vitelline strands are thicker posteriorly than anteriorly.

The uterus in mature segments is of the usual type, viz., a narrow hollow stem lying in the median longitudinal line of the proglottis, continuous with the uterine canal, and with no openings to the exterior. In ripe proglottides, on the other hand (fig. 2), the hollow median stem has become dilated into a broad trunk of considerable size (occupying a fifth or sixth of the breadth of the proglottis and most of the space between the dorsal and ventral surfaces), the wall of which bears irregular lateral very short lobose protuberances, the whole cavity being filled with eggs. Serial transverse sections also reveal the fact that at this stage the uterus opens to the exterior by a single very large and conspicuous ventral pore, situated anterior to the cirrus sac level and nearly midway between this and the anterior limit of the proglottis. I am not certain as to whether other additional pores are subsequently formed (and the ventral uterine wall approaches very close to the ventral subcuticula in two or three places, though no openings were present in my sections) but I doubt it, both because the proglottides appear to be fully ripe and because of the large size of the very well-defined single existing pore. The uterine eggs measure about 22 microns in external diameter, the embryos about 11 microns.

In transverse section the mature and ripe proglottides are seen to be extremely flat. Beddard remarks that in his immature specimens he could find 'no marked layer of longitudinal fibres in the body generally' and quotes Schwarz as saying that 'die innere





FIGS. 1, 2. *Proteocephalus marenzelleri*.

„ 3 to 7. *Proteocephalus naiae*.

- Fig. 1 ( $\times 12$ ). Scolex. Compare the magnifications of this and fig. 2, and figs. 3, 4 and 5.  
 Fig. 2 ( $\times 12$ ). Ripe proglottis. Dorsal view. The testes are degenerating. Note the small size of the uterine diverticula.  
 Fig. 3 ( $\times 87.5$ ). Scolex in outline.  
 Fig. 4 ( $\times 12$ ). Mature proglottis, unflattened. Dorsal view.  
 Fig. 5 ( $\times 12$ ). Ripe proglottis, much flattened. Dorsal view.  
 Fig. 6 ( $\times 180$ ). Ducts in the region of the ovarian isthmus. Ventral view.  
 Fig. 7 ( $\times 27.5$ ). Transverse section through a young ripe proglottis immediately in front of the ovary.

EE.—egg-ejector ('schluckapparat'); IL.—internal layer (sheath) of longitudinal muscles; IS.—isthmus of ovary; LMN.—longitudinal muscles of neck; N.—nerve; OV.—ovary; PA.—modified parenchymal core in medulla; SC.—nuclear layer of subcuticula; SH.—shell gland; T.—testes; UD.—uterine canal; UDO.—opening of uterine canal into median chamber of uterus sac; UTO.—opening of uterus to exterior; V.—vitellaria; Va.—vagina.



Längsmuskulatur ist schwach.' In all my sections through mature and ripe proglottides there is a very distinct layer of internal longitudinal muscles—much more distinct than that in Beddard's '*Solenotaenia*' *viperis* (*vide infra*), because definite bundles of two, three or more fibres are present and are relatively numerous. The medulla contains a core of specialized parenchyma in which the meshes are transversely elongated. I only observed the specialized longitudinal musculature of the neck region in a toto-preparation.

***PROTEOCEPHALUS NAIÆ* (Beddard, 1913)**

Syn., *Ophidotaenia naiae* Beddard, 1913.

Of this species I possess more than two dozen specimens, all taken from the anterior and middle intestines of ten (fourteen examined) full-sized cobras (*Naia tripudians*), supplied by snake-charmers of the United Provinces, India. This species has already been described by Beddard (1913a) from three specimens obtained from a cobra which died in the Zoological Gardens, London, but a re-description is necessary owing to the original account being deficient in some respects. Most of my specimens were found in the intestine just behind the stomach and isolated detached proglottides were also found in the faeces on several occasions. My largest (unflattened) specimen measured 180 mm. in total length, with a maximum breadth of 2.5 mm., but other specimens (mostly without ripe proglottides) measured considerably less and one immature specimen only measured 43 mm. Beddard's largest specimen measured 110 mm., with a maximum breadth of 1.5 mm.

In the following account of the species I shall for the most part only deal with those features which require a more complete description than Beddard has given, or which, in my opinion, have been misunderstood by him. As Beddard remarks, the 'rostellum' (by which term I mean simply the terminal part of the scolex, anterior to the suckers) is never very conspicuous (fig. 3) and when retracted consists solely of a very restricted non-projecting area lying between the suckers. In my specimens (toto- and in sections), as in Beddard's, an apical body is absent, though a number of gland-like cells appear to be clustered in the position normally occupied by

the apical organ. Cuticular spinelets were absent. In seven of my balsam preparations, the scolex measured 0.248 to 0.303 mm. in breadth and 0.153 to 0.201 mm. in length (from apex to lower edge of suckers), and the maximum diameter of the suckers varied between 0.106 mm. and 0.153 mm. The suckers are borne on lobes of the scolex base (each sucker, however, occupying the bulk of the lobe) and are undoubtedly protrusible. The unsegmented neck in my specimens is of considerable length, varying between 3.5 mm. (in one case) and 6 mm. (in most cases) according to the state of contraction, and 0.116 to 0.614 mm. in breadth. According to Beddard the neck is 'short.'

The mature and ripe proglottides are of considerable size and are only found in the extreme hind regions of most worms, the greater part of the strobila being composed of large and yet immature proglottides. Only in one of my two dozen specimens were the proglottides in a ripe condition. The immature proglottides (unflattened) in most worms varied between  $\frac{2.242 \text{ mm. broad}}{0.295 \text{ mm. long}}$  and  $\frac{1.770 \text{ mm. broad}}{1.121 \text{ mm. long}}$ , and more or less mature proglottides between  $\frac{2.655 \text{ mm. broad}}{0.413 \text{ mm. long}}$  (considerable contraction) and  $\frac{0.531 \text{ mm. broad}}{3.009 \text{ mm. long}}$  (considerable extension), but the average shape of the mature and ripe proglottides is square or a little longer than broad (figs. 4, 5). The genital openings are irregularly alternate and open, often on a distinct projection, either midway in the length of the proglottis or a little anterior to this point. The cirrus sac and vagina irregularly alternate as to which is anterior. The cirrus sac, in unflattened and not unduly contracted or extended proglottides, extends across about a quarter of the breadth of the proglottis and, when fully developed, measures about 0.498 to 0.531 mm. long and 0.083 to 0.107 mm. broad. In flattened (between glass slides) and very contracted or extended proglottides the sac varies enormously in size, from being almost globular in form and therefore very short, to very elongated in form and extending across at least one-third the width of the proglottis. In the cirrus sac both the cirrus (unarmed) and the ductus are usually coiled. In many of my flattened proglottides the cirrus is everted to its full extent and in some cases is longer than one-third the width of the proglottis,

and then the sac is practically invisible, from which I conclude (though the eversion may have been due to the artificial flattening) that, in these cases at least, the cirrus sac itself has been everted, though Beddard says that he has seen no evidence of this. The wall of the cirrus sac is thin but muscular. A small cloaca genitilis is present. The coils of the vas deferens in unflattened preparations are not very voluminous and are just visible as far as the middle line of the proglottis. In elongated proglottides the vas deferens coils form a bunch in the middle line. The vagina opens at the same horizontal level as the cirrus, but away from the opening it lies ventral to the cirrus sac and to the vas deferens coils. The vagina is very slightly dilated near its opening but in no other region and, except in very elongated proglottides, is sinuous or slightly convoluted just anterior to the ovary. The testes are about 120 in number and in unflattened preparations measure, on the average, about 62 by 36 microns. They are situated in two quite separate lateral fields. The vitellaria (cir. 14 by 11 microns) are, as usual, arranged in two thin lateral strands, which, however, are distinctly broader posteriorly than anteriorly. The ovary consists, as usual, of two lobes connected medianly by an isthmus. In surface view the lobes are narrow antero-posteriorly and extend laterally, in mature proglottides, only a little more than half-way to the proglottis edge. In sections they are seen to be very thin dorso-ventrally and to lie nearer the dorsal than the ventral surface of the strobila, though the isthmus connecting the lobes bends ventrally to allow of the dorsal passage of the uterine canal and vagina. The lobes are distinctly follicular. Beddard says that he 'could not find any signs of a shell-gland' and he endeavours to correlate its supposed absence with the presence of a 'glandular investment' on the walls of the uterine diverticula, which he assumes to take the place of a shell-gland. For my part, I have had no difficulty in finding a very distinct shell-gland (diagrammatically represented in fig. 6) in most of my preparations, and, on the other hand, I have been unable to find any investment of the uterine walls with cells which can be described as glandular. A distinct egg-ejector ('schluckapparat') is also present. The uterus in my ripe proglottides (fig. 5) consists of (a) a wide median uterine sac extending the whole length of the proglottis from the ovary anteriorly, which carries on either side from 16 to 25 lobose diverticula



of very different sizes (I could not detect any diverticula ventral to the ovary), and (b) a uterine canal, which, with the vagina, passes *dorsal* to the ovarian isthmus, and opens into the median uterine sac some distance in front of the ovary. Nearly all the eggs are collected in the diverticula, in which they are freely scattered (not in clusters), and they possess two distinct shells, the outermost thick shell measuring about 25.6 microns in diameter, and the contained embryo 9 to 11 microns. The median sac of the uterus has a number of pointed downgrowths (fig. 7) which open on what is usually considered to be the ventral surface of the strobila. The position of the uterine pores is indeed the sole certain criterion of determining the orientation of the strobila.

In transverse sections (fig. 7) through mature proglottides the usual two layers of longitudinal muscles are to be seen—a very thin layer just external to the nucleated region of the subcuticula and internal to an equally thin circular muscle layer, and a thicker, though somewhat attenuated, internal layer of longitudinal muscles, demarcating the cortex from the medulla. The parenchyma is in most regions of a uniform wide-meshed character, but in the centre of the medulla there is a kind of core of closer-meshed parenchyma, with the meshes transversely elongated. This core of differentiated parenchyma is apparently identical with that figured by Beddard (1913b, p. 167, text-fig. 38) for '*Ichthyotaenia* sp.' (i.e., *P. marenzelleri*) only Beddard assumes (in the absence in his immature specimens of an internal longitudinal muscle sheath) that it represents the whole of the medulla, whereas in *P. naiaae* and in my mature specimens of *P. marenzelleri* (*vide supra*) it is obviously only the internal region of it. I am ignorant of the significance of this altered parenchymal core.

***PROTEOCEPHALUS VIPERIS* (Beddard, 1913)**

Syn., *Solenotaenia*  *viperis* Beddard, 1913.

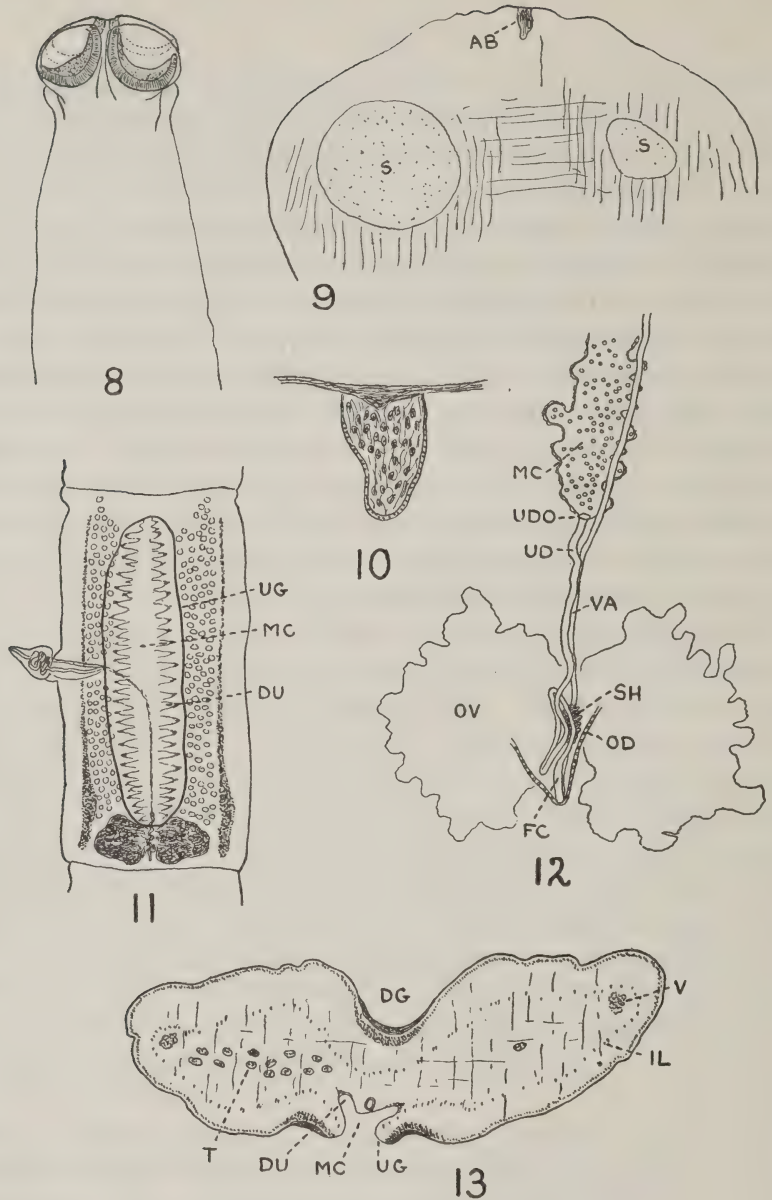
Beddard (1913c) has provided a full description of this remarkable species, and the following account only professes to supply details which Beddard has omitted and to confirm and, if possible, emphasize, his statement of the peculiar character upon which he founded his new genus *Solenotaenia*. I possess a large number of specimens

of this species contained in the helminthological collection made by Dr. L. W. Sambon almost entirely from animals which had died in the London Zoological Gardens, and now in the Wellcome Bureau of Scientific Research.

*Proteocephalus viperis* (as I propose to call this species) is a parasite of the Crossed Viper, *Lachesis alternatus*, from Central or South America. One nearly-entire worm in my collection measured 170 mm. in total length (in spirit) and others must have reached 200 mm. and possibly more, so that my specimens were somewhat longer than those studied by Beddard. The maximum breadth of my specimens was 2.41 mm., and was always found in the region of immature proglottides. Mature and ripe proglottides only occur in about the last quarter of the worm's length. There are no external signs of segmentation, save the small lateral notches and the uterine grooves which demarcate ripe proglottides.

The scolex (fig. 8) consists almost entirely of the four large hemispherical suckers, which occupy the greater part of the four lobes which bear them. The terminal area between the suckers is extremely small and does not protrude. The scolex measures 0.860 to 1.527 mm. in breadth and 0.531 to 0.713 mm. in length (from tops to bases of suckers). The suckers measure 0.415 to 0.664 mm. in breadth and look upwards and outwards. Spinelets are entirely absent. As Beddard remarks, a minute funnel-shaped apical organ is present, which is so small that it is almost invisible in toto-preparations. Its appearance, in longitudinal section, is shown in figs. 9 and 10. An unsegmented neck is present, varying in different specimens from 1.7 mm. to 4.7 mm. in length and 0.767 to 1.534 mm. in breadth, but the average length is about 3 mm.

As already remarked, the broadest part of the strobila is in the region of immature proglottides. The proglottides are here indicated by the presence of faint transverse segmentation lines and more posteriorly by genital rudiments and are all much broader than long, measuring from  $\frac{2.419 \text{ mm. broad}}{0.236 \text{ mm. long}}$  and  $\frac{2.124 \text{ mm. broad}}{0.088 \text{ mm. long}}$  to  $\frac{1.534 \text{ mm. broad}}{0.354 \text{ mm. long}}$  (all measurements of unflattened material). Mature and ripe proglottides are not nearly so broad, the former being either



FIGS. 8 to 13. *Proteocephalus viperis*.

Fig. 8 ( $\times 17.5$ ). Scolex in outline.

Fig. 9 ( $\times 56$ ). Longitudinal section through the scolex showing the minute apical organ.

Fig. 10 ( $\times 260$ ). The apical organ in longitudinal section.

Fig. 11 ( $\times 27.5$ ). Ripe proglottis with the uterus entirely split along its whole length and empty of eggs. Note the small diverticula.

Fig. 12 ( $\times 56$ ). Ducts in the region of the ovary, from the dorsal view. In this proglottis the uterus has not yet split to the exterior.

Fig. 13 ( $\times 39$ ). Transverse section through a ripe proglottis behind the cirrus sac. Note the open uterus, the small uterine diverticula and the weak internal longitudinal muscle sheath.

AB.—apical organ; DG.—dorsal groove (artefact ?); DU.—diverticula of uterus; FC.—fertilization chamber; IL.—internal layer (sheath) of longitudinal muscles; MC.—median chamber of uterus; OD.—oviduct (?); OV.—ovary; S.—sucker; SH.—shell-gland; T.—testes; UD.—uterine canal; UDO.—opening of uterine canal into median chamber of uterus sac; UG.—uterine groove, edge of; V.—vitellaria; VA.—vagina.



approximately square in shape or longer than broad, and measuring from  $\frac{1.121 \text{ mm. broad}}{0.885 \text{ mm. long}}$  to  $\frac{1.534 \text{ mm. broad}}{1.888 \text{ mm. long}}$  and  $\frac{1.230 \text{ mm. broad}}{2.006 \text{ mm. long}}$ , and the latter (fig. 11) always being longer than broad and measuring from  $\frac{0.885 \text{ mm. broad}}{1.652 \text{ mm. long}}$  to  $\frac{1.357 \text{ mm. broad}}{4.838 \text{ mm. long}}$ . In my material the genital apertures are situated almost on the middle transverse line of the proglottis but not quite, being a little in front, and the cirrus aperture is usually in front of the vaginal, though the reverse condition does occur. The cirrus sac is very broad antero-posteriorly and measures in my preparations 0.298 to 0.365 mm. in length and 0.149 to 0.182 mm. in breadth, and it extends across from one quarter to one-third of the breadth of the proglottis according to the state of contraction of the latter. The cirrus sac wall is very thin, though quite well-defined, and apparently contains no muscle-fibres. The sac contains three parts of the cirrus apparatus: (a) an external thick-walled convoluted part which forms the outer walls of the extruded cirrus, (b) a long thick-walled (less thick than the first part) straight tube (the cirrus canal), and (c) coils of the ductus. The first two parts have attached to them ejector muscle-fibres (Beddard's 'layer of glandular cells'?). The cirrus when everted (which may equal in length half the breadth of the proglottis) is slender distally but dilated at the base which contains the ductus coils (fig. 11), and the sac, contained inside the proglottis in this condition, is relatively narrow (only 0.041 mm. broad and 0.298 mm. long in one specimen which reached a quarter of the distance across the proglottis). The sac itself then is not everted. The cirrus is not armed. The coils of the vas deferens are not very voluminous and extend to about the middle of the proglottis. The vagina opens on the same horizontal level as the cirrus and shows no marked dilatation anywhere in its course, though in contracted proglottides (not in extended) it becomes convoluted anterior to the ovary. It occasionally opens on a papilla and there is no genital atrium. The ovary in mature non-elongated proglottides is only a little more than half the breadth of the proglottis and is of the shape shown in fig. 11. There is no narrow canalicular isthmus, the follicles of the ovary extending across the middle line over a broad area. The vitellarian strands (thickened posteriorly)

have been sufficiently described by Beddard, and are of course medullary in position. The testes, as Beddard states, are very numerous, lie in two distinct fields, and measure in toto-preparations about 44 by 25 microns. I must also mention that both the vagina and the uterine canal (*vide infra*) lie on the dorsal side of the ovary (the former lying for the most part ventral to the latter), that in two of my preparations the oviducts\* apparently join the vagina at the level of the hind end of the ovary (an unusual position) and that there is a recognizable shell-gland. In fig. 12 I have depicted these ducts as well as I am able to make them out, but I cannot guarantee the exact positions of the coils, nor could I detect the vitelline ducts.

Beddard has fully described the uterus and its extraordinary later development in this species, and I intend only to make one or two corrections in his account and to emphasize the features in which this uterus differs from that of other known Proteocephalidae. As Beddard says, the early development of the uterus as a median hollow stem is like that of other Proteocephalids, but he omits to lay stress upon the fact that whereas the uterus of most other Proteocephalids remains devoid of eggs until the diverticula are well developed, the uterus of '*Solenotaenia*' (like that of *P. marenzelleri* and some other snake Proteocephalids) becomes crammed with eggs while the diverticula are either entirely absent or only represented by minute irregularities of the wall (fig. 12). This fact in itself indicates that the '*Solenotaenia*' uterus is distinct from that of the majority of Proteocephalids. The next stage of development of the '*Solenotaenia*' uterus is, not the development of large diverticula, but the splitting and opening to the exterior of its entire ventral wall (the process commencing anteriorly and proceeding posteriorly, until the entire length is exposed), so that the whole cavity of the stem uterus becomes continuous with the outer world and in consequence devoid of the eggs which are at once liberated (figs. 11, 13). There is thus formed, as the final stage of development of the uterus, a deep and broad uterine groove, with smooth thickened edges, situated on the ventral side of the proglottis along nearly its entire length, i.e., from the posterior opening of the uterine duct to near

\* These ducts (which are very distinct in one preparation) may possibly be the vitelline ducts, though they appear to come from the ovary and I cannot trace any connection with the vitellaria. I also admit that I cannot see these ducts in most of my preparations, nor in serial transverse sections.

the anterior end of the proglottis. This conspicuous uterine groove, as Beddard points out, is quite distinct morphologically from the apparently similar longitudinal grooves in certain Bothriocephalids and in many Proteocephalidae, since in these latter it is only a continuous depression of the body-wall which harbours the uterine pores, whereas in the former it is equivalent to the fused uterine pores themselves and represents the actual cavity of the uterus. Correlated with this formation of the uterine groove\*

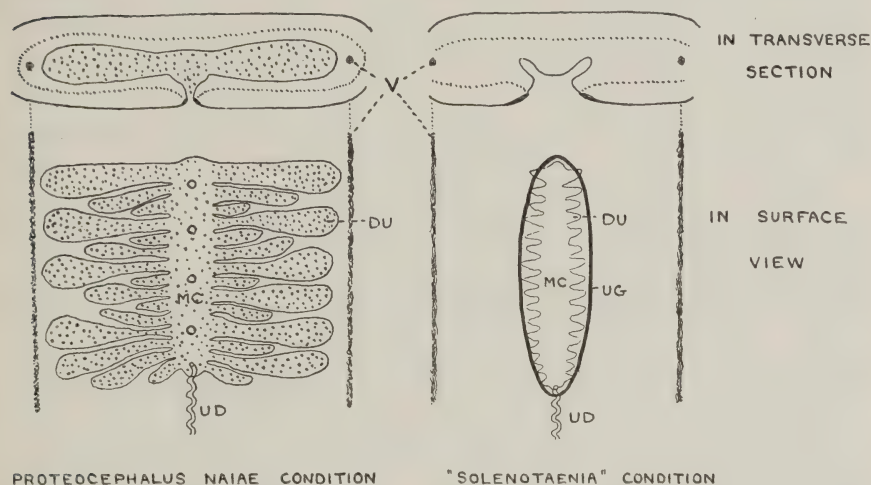


DIAGRAM to contrast the conditions of the ripe uteri of a normal Proteocephalid and of "*Solenotaenia*."

DU.—diverticula of uterus; MC.—median chamber of uterus; UD.—Uterine canal; UG.—uterine groove, edge of; V.—vitellaria.

in '*Solenotaenia*' and the early formation of the large uterine pores in allied species is the stunted development of the diverticula which are so conspicuous a feature in the fully-formed uteri of most other Proteocephalids. This difference of development of the uterus in this species, compared with the developments of the uteri of most other Proteocephalids, would afford a very much better basis for the founding of a distinct genus (cf. Lühe's characterization of the genera of the Ptychobothriinae e.g.) than the trivial scolex characters,

\* In my figure 13 of a transverse section it will be observed that there is, in my material, a very distinct dorsal groove bordered by a thickened area of the subcuticula. This dorsal groove is possibly the result of local contraction, since Beddard's figures do not indicate its presence in his material.



and even the testes distribution, which have been utilized up to the present, and I would readily adopt Beddard's new genus *Solenotaenia* were it not for the facts that: (1) the stunted uterine diverticula found in '*Solenotaenia*' are also to be found in several other Ophidian Proteocephalids which do not possess the uterine groove (e.g., in *P. marenzelleri*, *P. calmettei* and '*Crepidobothrium gerrardii*'), and that (2) there appears to be every transition from these stunted diverticula (cf. e.g., *P. racemosa*, *P. nattereri* and the '*O. monnigi*' recently described by Fuhrmann, 1924) up to fully-developed diverticula (as in the '*O. punica*' recently re-described by Southwell and Adler, 1923, and many other species of '*Ophiotaenia*'), and that (3) the uterine groove represents physiologically, if not morphologically, after all only a fusion of uterine pores and is therefore only an individual, i.e., specific, peculiarity of an external character.

Beddard says nothing about the development of the uterus into two definitive portions—the dorsal *uterine canal*\* (representing the posterior portion of the primitive stem) and the ventral *uterine sac*—a development common to many other Proteocephalids, though not to all. He, however, states that in this species and in '*Ophidotaenia naiae*' (= *Proteocephalus naiae*, *vide supra*) the minute and large uterine diverticula respectively are invested with cells which seem to be 'exactly like those of the shell-gland in other tape-worms,' and he suggests that they may have a similar function, i.e., that the eggs may, in these two species, acquire their shells in the uterus instead of in the usual place. I have observed these cells investing the uterine wall in *P. viperis*, but I am not convinced of their glandular nature, and, as Beddard remarks, a shell-gland is apparently present in '*Solenotaenia*,' and is certainly present in *Proteocephalus naiae*, though Beddard failed to observe it in this latter case.

The fully-formed eggs of *Proteocephalis viperis* are fairly thick-shelled and measure about 21.7 microns in diameter, and the contained hooked embryos about 12.8 microns. In transverse section (fig. 13) the general parenchyma of the proglottis is seen to be wide-meshed and to be divided into the usual two regions of cortex and medulla by the presence of a very weakly-developed internal

\* Beddard apparently figures this canal in transverse section in his text-figure 50 (p. 252) but is under the impression that it represents a convolution of the vagina. In my serial transverse sections I have followed both ducts through their entire course and have seen the uterine canal opening into the uterus sac.

layer of longitudinal muscles, a layer consisting of widely-separated small bundles, each containing only two or three fibres, and occasionally of single fibres.

The foregoing three species are provisionally placed in the genus *Proteocephalus* (syn. *Ichthyotaenia*) and not in '*Ophiotaenia*' (La Rue, 1911) or '*Crepidobothrium*' (vide Nybelin, 1917) for the reasons stated by me in a paper published elsewhere (Woodland, 1925).

#### REFERENCES

- BARROIS, T. (1898). 'Sur quelques Ichthyoténias parasites des Serpents.' *Bull. Soc. Sci. Agric. et Arts. Lille*. T. 2, p. 4. (The present writer has not been able to see this paper.)
- BEDDARD, F. E. (1913a). 'Contributions to the Anatomy and Systematic Arrangement of the Cestoidea. VII. On Six Species of Tapeworms from Reptiles belonging to the Genus *Ichthyotaenia* (s.l.).' *Proc. Zool. Soc. London*, Part I, p. 4.
- (1913b). 'Contributions, etc. VIII. On some Species of *Ichthyotaenia* and *Ophidotaenia* from Ophidia.' *Ibid.*, p. 153.
- (1913c). 'Contributions, etc. IX. On a new Genus of Ichthyotaeniids.' *Ibid.*, p. 243.
- FUHRMANN, O. (1924). 'Two new Species of Reptilian Cestodes.' *Ann. Trop. Med. and Parasitol.*, Vol. XVIII, No. 4, p. 505.
- LA RUE, G. R. (1911). 'A Revision of the Cestode Family Proteocephalidae.' *Zool. Anzeig.*, Bd. 38, p. 473.
- (1914). 'A Revision of the Cestode Family Proteocephalidae.' *Illinois Biological Monographs*, Univ. of Illinois, Vol. I, Nos. 1 and 2.
- NYBELIN, O. (1917). 'Results of Dr. E. Mjöberg's Swedish Scientific Expedition to Australia, 1910-1913. XIV. Australische Cestoden.' *Kungl. Svenska Vetén. Handl.* Bd. 52, No. 14.
- SCHWARZ, R. (1908). 'Die Ichthyotaenien der Reptilien und Beiträge zur Kenntnis der Bothriocephalen.' *Inaug.-Dissert. Univ. Basle*. 52 pp. and 7 plates.
- SOUTHWELL, T., and ADLER, S. (1923). 'A Note on *Ophiotaenia punica* (Cholodovski, 1908) La Rue 1911.' *Ann. Trop. Med. and Parasitol.*, Vol. XVII, p. 333.
- WOODLAND, W. N. F. (1925). 'On three new Proteocephalids and a Revision of the Genera of the Family.' *Parasitology*, Vol. XVII, p. 295.